

Acknowledgements

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The reproductive strategies of edible-nest swiftlets (*Aerodramus* spp.)

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The Black-nest Swiftlet *Aerodramus maximus* and the White-nest Swiftlet *A. fuciphagus* are important commercially in south-east Asia as their nests are collected extensively for use in Chinese cuisine and medicine (see Kang *et al.* 1991). They are sympatric in many areas

(King *et al.* 1975) and are similar in some aspects of their behaviour and ecology. Both are aerial insectivores exploiting overlapping feeding niches (Waugh & Hails 1983), and nest colonially in caves or suitable man-made structures (Kang & Lee 1991). The breeding biology of the Black-nest Swiftlet has been studied in Sarawak (Medway 1962a,b, Harrisson 1974), and the White-nest Swiftlet in Penang (Langham 1980). In Singapore, Black- and White-nest Swiftlets often form mixed-species nesting colonies, allowing us to compare reproductive behaviour of the two species under similar conditions. The Black-nest Swiftlet normally lays one egg per clutch while the White-nest Swiftlet lays two. How Black- and White-nest Swiftlets may benefit reproductively from the difference in their clutch-sizes was investigated by clutch manipulation experiments and studying the effect of these experiments on reproductive success. Our results indicate that the clutch-sizes of the two species may be influenced by two factors: (1) the ability of the adults to raise the nestlings, and (2) the insurance against reproductive failure that is provided by laying more than the usual number of eggs in the clutch.

MATERIALS AND METHODS

We studied four mixed-species colonies on the island of Sentosa off the southern coast of Singapore (1°09'N, 13°45'E) in April–June 1984. Twenty-nine 'white' nests belonging to White-nest Swiftlets and 60 'black' nests occupied by Black-nest Swiftlets were numbered and the progress of the clutches contained in them monitored by visiting them twice or three times a week. Disturbance to the colonies was minimized by making the nest visits during the day when the adult birds were absent. Nestlings were weighed with a 10 g or 50 g Pesola balance, and wing-length (as defined by King *et al.* 1975) measured to the nearest mm. The age of nestlings was estimated using the method of Ricklefs (1975). Using measurements obtained from 58 Black-nest Swiftlet nestlings and 48 White-nest Swiftlet nestlings, a graphical plot of wing-length against age was made for each species, and was used for estimating age of subsequent nestlings.

Clutch manipulation experiments were carried out on both species. Care was taken not to disturb the breeding birds by performing the manipulations when the parent birds were away from the colony. Ten additional 'black' and 'white' nests were selected in which the normal clutch-size was enlarged by adding an extra egg. Thus each 'black' nest contained two eggs instead of one, and each 'white' nest three eggs instead of two. The age difference between the added egg and the original clutch ranged from 0 to 9 days. One egg was also removed from another ten 'white' nests, leaving one egg per nest instead of two. Once the clutch had been either 'enlarged' or 'reduced', its progress was monitored to the end of the experiment; lost eggs or nestlings were not replaced. The effects of disturbance caused by the clutch manipulations on the birds were controlled by handling eggs and nestlings from manipulated and non-manipulated nests which contained the normal clutch-sizes in the same way: eggs and nestlings were measured and

TABLE 1

Comparison of the breeding chronologies of Black- and White-nest Swiftlets. The data are presented as mean, s.d. (n). Incubation and fledging periods are calculated using the method of Medway (1962a). The incubation period for the White-nest Swiftlet is the time taken from the laying to the hatching of the first egg; the fledging period is the time taken from the hatching of a nestling to its leaving the nest. For the White-nest Swiftlet, the fledging period is the mean for first and second nestlings combined

	Duration (days)	
	Black-nest Swiftlet	White-nest Swiftlet
Laying interval	—	3.3, 0.4 (7)
Hatching interval	—	3.3, 0.9 (21)
Incubation	25.5, 2.2 (11)	25.1, 0.3 (4)
Fledging	45.9, 2.6 (41)	39.8, 2.6 (20)

weighed and the reproductive success of manipulated nests was compared with non-manipulated nests. Statistical analysis of the data was based on methods described by Sokal & Rohlf (1969), using the statistical computer package SPSS/PC⁺ (Norusis 1986).

RESULTS

Breeding chronology

Table 1 summarises the breeding chronologies of the two species of swiftlets. The interval between laying the first and second egg for White-nest Swiftlets was found to be around three days, consistent with results reported by Langham (1980). Incubation of the eggs began after the first egg was laid. The two eggs hatched asynchronously with a hatching interval of about three days. The incubation period was similar for the two species ($t=1.69$, $df=9$, $P>0.05$), but the fledging period was longer by around six days for Black-nest Swiftlets ($t=8.53$, $df=23$, $P<0.05$).

Nestling growth

Figures 1 and 2 show the graphical plot of body mass and wing length against age for the Black- and White-nest Swiftlet, respectively. In both species nestling growth, as measured by body mass, appeared to follow a sigmoid curve. Using the method described by Ricklefs (1967, 1983), the Logistic equation was found to provide the best fit to the curve and takes the form:

$$M(t) = A \{1 + \exp[-K(t - t_i)]\}^{-1}$$

where $M(t)$ = body mass (g) at age t , A = asymptotic or peak nestling body mass (g), K = growth rate (per day), t = nestling age (days) and t_i = age at the point of maximum growth rate (days).

The various nestling growth parameters as described by the Logistic equation are summarised in Table 2. There appears to be little difference in the growth rates between the first and second nestlings of White-nest Swiftlets.

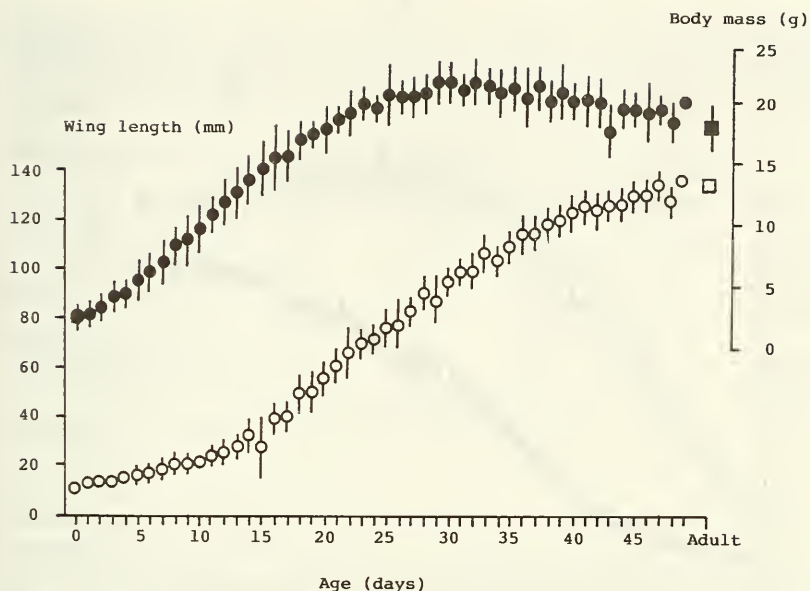


Figure 1. Increase in body mass (●) and wing length (○) of Black-nest Swiftlet nestlings. Adult body mass (■) and wing length (□) are shown. Mean and s.d. (vertical line) are given. Data derived from 58 nestlings.

Clutch manipulation and reproductive success

Three parameters were calculated as indicators of reproductive success: hatching success, nestling mortality and a reproductive index, R , expressed as the mean number of nestlings raised per pair of adults per brood. Hatching success was defined as the percentage of all eggs being monitored that hatched, nestling mortality as the percentage of nestlings that died or disappeared from the nest before they were due to fledge. The reproductive index R combines the effects of hatching success and nestling mortality. Table 3 shows the reproductive success of Black- and White-nest Swiftlets with normal-sized and manipulated clutches. For Black-nest Swiftlets, hatching success was not significantly changed but nestling mortality was significantly increased in 'enlarged' clutches when compared with normal-sized clutches ($\chi^2=13.91$, $df=1$, $P<0.05$). R was, however, not significantly different between normal-sized and 'enlarged' clutches (one-way ANOVA, $F=2.23$, $df=1,68$, $P>0.05$). In contrast, for the White-nest Swiftlet, neither enlarging nor reducing the clutch-size appeared to affect hatching success or nestling mortality significantly ($\chi^2=0.17$, $df=1$, $P>0.05$), but R was significantly larger in 'enlarged' clutches than in 'reduced' clutches (one-way ANOVA, $F=3.46$, $df=2,46$, Student-Newman-Keuls range test, $P<0.05$).

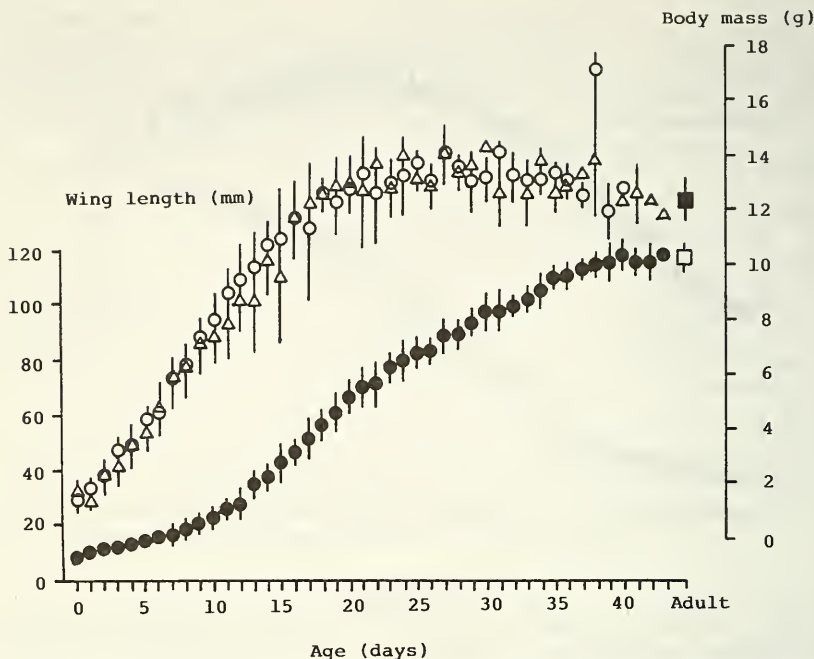


Figure 2. Increase in body mass of first (○) and second (△) nestlings and wing length (●) of White-nest Swiftlet. Adult body mass (■) and wing length (□) are shown. Mean and s.d. (vertical line) are given. Data derived from 48 nestlings. Day 0 for both first and second nestlings is taken as the day on which each nestling hatched.

TABLE 2

Comparison of nestling growth parameters of Black- and White-nest Swiftlets. K=growth rate; A=asymptotic body mass; t_{10-90} =time taken for growth from 10 to 90% A; N=the number of nestlings from which data were obtained

	Black-nest Swiftlet	White-nest Swiftlet	
		1st nestling	2nd nestling
K (per day)	0.178	0.214	0.210
A (g)	22.0	14.5	14.5
Days to reach A	29	28	31
T_{10-90} (days)	25	20	21
N	58	28	20

DISCUSSION

In tropical species of birds of less than 100 g the value of K typically ranges from 0.278 to 0.520 (Ricklefs 1976). Thus, by comparison, the

TABLE 3

Reproductive success of Black- and White-nest Swiftlets with normal sized (N), 'reduced' (RE) and 'enlarged' (E) clutches. N_1 =total number of eggs; N_2 =total number of nestlings; N_3 =total number of nests. Fledging success is expressed as 100% - nestling mortality. Reproductive index, R, is expressed as the number of nestlings (mean, s.d.) raised per adult pair per brood

Clutch size	Black-nest Swiftlet		White-nest Swiftlet		
	1 (N)	2 (E)	1 (RE)	2 (N)	3 (E)
N_1	60	20	10	58	30
Hatching success (%)	97	85	90	83	80
N_2	58	17	9	48	24
Nestling mortality (%)	24	71	56	58	50
Fledging success (%)	76	29	44	42	50
N_3	60	10	10	29	10
R	0.73, 0.45	0.50, 0.53	0.40, 0.52	0.69, 0.76	1.20, 0.63

Black-nest Swiftlet ($K=0.178$) and the White-nest Swiftlet ($K=0.214$) have slow growth rates. In nature, both species of swiftlets nest in caves, which tends to exclude most predators of nestlings except man (Medway 1963). The reduced risk of predation may have lifted the selection pressure for fast growth rates (Case 1978). In addition, aerial insectivory may select for slow growth rates as an adaptation to periods of food shortages, because flying insects tend to be an unstable and unpredictable food source (Ricklefs 1969).

Black- and White-nest Swiftlets apparently differ in their reproductive strategies. The Black-nest Swiftlet lays a single, larger egg per clutch (see Kang *et al.* 1991) and apparently concentrates its reproductive effort on the single nestling, as suggested by the clutch manipulation experiments. Whilst it was usually able to raise its normal-sized clutch of one successfully, there was a significant increase in nestling mortality in the 'enlarged' clutches (Table 3).

In contrast, the White-nest Swiftlet lays two smaller eggs per clutch, with a shorter average fledging period than the Black-nest Swiftlet (Table 1) which may increase the possibility of multiple layings (Bryant & Hails 1983). Its reproductive strategy appears to be more opportunistic than that of the Black-nest Swiftlet. In the clutch manipulation experiments, neither hatching success nor nestling mortality was significantly changed in either 'reduced' or 'enlarged' clutches when compared to normal-sized clutches. R was statistically different between 'reduced' and 'enlarged' clutches, with an intermediate value for normal-sized clutches (Table 3). The increase in R in 'enlarged' clutches of the White-nest Swiftlet is in contrast to the Black-nest Swiftlet, where despite the additional egg, R in the 'enlarged' clutches was not significantly different from normal-sized clutches.

The differences in the effect of clutch-size enlargement on the reproductive success of Black- and White-nest Swiftlets may be related to the availability of food for the additional nestlings. Aerial insect density and

diversity tend to be higher and more stable near the ground or canopy levels than at higher altitudes (Medway 1962a,b, O'Connor 1975, Hails & Turner 1985). The heights at which different species of aerial insectivores feed may be indicated by two measures of the degree of manoeuvrability in flight: Tail Index (ratio of tail length to body mass) and Wing Index (ratio of wing length to body mass). As suggested by Waugh & Hails (1983) and Hails & Amiruddin (1981), a larger index may indicate a higher degree of manoeuvrability that is advantageous for species that feed close to vegetation. We were unable to observe either species of swiftlets feeding during the day as individuals marked with small coloured streamers did not remain within our range of visibility and the two species are difficult to separate in the field. But measurements of 60 Black- and 54 White-nest Swiftlets showed that they differed significantly in both Tail (one-way ANOVA, $F=575.77$, $df=1,112$, $P<0.01$) and Wing Indices (one-way ANOVA, $F=514.33$, $df=1,112$, $P<0.01$). White-nest Swiftlets (Tail Index 4.3, Wing Index 9.8) may well be more manoeuvrable in flight than Black-nest Swiftlets (Tail Index 2.5, Wing Index 6.6). Hence it is possible that White-nest Swiftlets, morphologically better adapted to feeding at lower heights than Black-nest Swiftlets, may exploit a wider range of feeding niches, and are thus less affected than Black-nest Swiftlets by an increased nestling demand caused by artificial enlargement of the clutch.

In nature, however, few Black- or White-nest Swiftlets lay larger than usual clutches. A possible factor limiting clutch-size in both species is the shortage of energy or depletion of stored lipids which may be faced by females during egg formation (see Kang *et al.* 1991). In addition, despite the variety of potential feeding niches available to White-nest Swiftlets, the adults may usually not be able to feed more than two nestlings at a time, as in none of the artificially enlarged clutches did all the nestlings fledge. Therefore the White-nest Swiftlet's clutch of two may represent the compromise between producing more eggs but not having the resources to rear all nestlings to the fledging stage, and producing fewer eggs but losing the insurance against reproductive failure that is provided by laying more eggs. In contrast, the Black-nest Swiftlet's clutch of one may be one solution to the combined problems of not having the resources to rear more than one nestling to the fledging stage, and not benefitting from the insurance against reproductive failure that is provided by laying more eggs.

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Plumage variation and geographical distribution in the Kalij and Silver Pheasants

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The genus *Lophura* Fleming consists of ten species of fowl-like pheasants, commonly called gallo-pheasants. They are distributed along the Himalaya east of the Indus River to Bhutan and then on through Burma, Thailand, Laos, Cambodia and Vietnam to China (including Hainan) and also through Peninsular Malaysia to Sumatra and Borneo (Howard & Moore 1984, Sibley & Monroe 1990).